

THE STATUS OF *SMILODON* IN NORTH AND SOUTH AMERICA

Annalisa Berta¹

ABSTRACT. South American representatives of the sabercat genus *Smilodon* (Felidae, Machairodontinae, Smilodontini) are referred to a single species, *Smilodon populator* Lund, 1842, from Pleistocene (?Uquian, Ensenadan–Lujanian) localities in Argentina, Bolivia, Brazil, Ecuador, Peru, and Uruguay. North American *Smilodon* from Pleistocene (late Irvingtonian–Rancholabrean) deposits are also assigned to *S. populator*. Diagnostic characters of *S. populator* include: large size; skull with broad muzzle; upper canines strongly recurved; upper canines and cheek teeth with finely serrated anterior and posterior margins; P⁴ with very reduced protocone; mandible usually with single, large mental foramen; mandibular flange greatly reduced. Variation was noted in several characters; smaller size, triangular occiput, and P₃ were more common among middle Pleistocene (Ensenadan and Irvingtonian) samples of *S. populator*. During the late Pleistocene, South American populations displayed a larger mean size than their North American contemporaries.

Smilodon gracilis (Cope, 1880) is a more primitive related form known from the late Pliocene (Blancan) through the middle Pleistocene (Irvingtonian) of North America. The derived species *S. populator*, apparently evolved in North America during the middle Pleistocene (late Irvingtonian) and spread into South America. As in North America, *Smilodon* became extinct in the southern continent at the end of the late Pleistocene (Rancholabrean and Lujanian, respectively).

INTRODUCTION

Although *Smilodon* has been known from the Pleistocene of North and South America since the early part of the 19th century, no previous studies have critically compared samples from the two continents. Such comparisons are essential to an understanding of the phylogenetic interrelationships of this sabercat and they also serve to strengthen existing biostratigraphic correlations between the Americas during the Pleistocene. The present contribution is an evaluation of the status of *Smilodon* in North and South America with emphasis upon its South American record of occurrence.

ORGANIZATION AND METHODS

In addition to citations of the original publications of F. Ameghino and P.W. Lund, cross-references to compilations of their publications are given. The *Obras Completas y Correspondencia de Florentino Ameghino* edited by A.J. Torcelli consists of 24 volumes published between 1913 and

1926. The *Memorias sobre a paleontologia Brasileira Revisitas e comentadas por Carlos de Paula Couto* is a single volume of Lund's work published in 1950. These compilations include reproductions of most of the work of F. Ameghino and P.W. Lund, and have had wider distribution than many of the original publications.

The chronology and usage of South American late Cenozoic Land Mammal Ages follows that proposed by Patterson and Pascual (1972). From oldest to youngest, the Uquian, Ensenadan, and Lujanian Land Mammal Ages are presently included within the Pleistocene, with the Uquian straddling the boundary between the Pliocene and Pleistocene. Correlation of North and South American late Cenozoic Land Mammal Ages follows Marshall et al. (1982) and suggests the following correlations: Lujanian with late Rancholabrean, Ensenadan with early and middle Rancholabrean and middle and late Irvingtonian, and Uquian with late Blancan and early Irvingtonian.

Metrical data presented in this study should be interpreted with caution. The scope of this analysis necessitated the use of measurements published by others, although care was taken to eliminate those that were not directly comparable with the system of measurement utilized here and described by Merriam and Stock (1932). Samples were often very small; this was especially true for South American late Pleistocene populations which unlike their North American contemporaries were not homogeneous with respect to locality and in some cases possibly age. Statistics were computed through the use of the BMDP (Dixon and Brown, 1979) programs.

The following institutions are referred to in the text: AMNH, American Museum of Natural History, New York, New York; BM(NH), British Museum (Natural History), London, England; FMNH, Field Museum of Natural History, Chicago, Illinois; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMP, Museo Municipal de Ciencias Naturales y Tradicional de Mar del Plata, Mar del Plata, Argentina; MNHN, Museum National d'Histoire Naturelle, Paris, France; ROM, Royal Ontario Mu-

1. Department of Biology, San Diego State University, San Diego, California 92182-0063.

seum, Toronto, Ontario, Canada; UZM L, Peter W. Lund Collection, Universitets Zoologiske Museum, Copenhagen, Denmark.

HISTORICAL REVIEW

The discovery of sabercats in South America was first announced by Lund (1842) and was based on material recovered from late Pleistocene–Holocene cave faunas of Lagoa Santa in eastern Brazil. *Smilodon* and a single species, *S. populator*, were named from isolated teeth and associated metapodials. Earlier, Lund (1839a) erroneously referred some of this material to *Hyaena neogaea*. Since at the time of the original designation *Hyaena neogaea* was insufficiently defined and no type material was designated, this species is regarded as a *nomen nudum* following Paula Couto (1955).

Subsequently, additional sabercats of Pleistocene age were discovered in Argentina, Bolivia, Ecuador, and Peru. Most of these specimens were attributed to *Smilodon*, although a few were described as new genera and subgenera [i.e. *Smilodon* (*Prosmilodon*) Rusconi, 1929; *Smilodontidion* Kraglievich, 1948].

Méndez-Alzola (1941) provided the most detailed description of South American sabercats and referred the Argentine material to *S. bonaeriensis*. Paula Couto (1955) reviewed the literature and, on the basis of Brazilian material, distinguished at the subspecific level the South American *S. populator populator* from the North American *S. populator californicus*. Churcher (1967) examined some Argentine material and added supplementary information about the South American species which he referred to *S. neogaeus*. Hoffstetter (1952) contributed to our knowledge of *Smilodon* from Ecuador, while Churcher (written comm., 1981) is describing an excellent sample from the Talara tar seeps of Peru.

At present two species of *Smilodon* are recognized. The small, slender *S. gracilis* is recorded from late Pliocene–middle Pleistocene (late Blancan–late Irvingtonian) localities in North America (Berta, in press). The large, robust, and more derived *S. populator* (synonyms include *S. floridanus* Leidy, 1889, *S. californicus* Bovard, 1907, and *S. fatalis* sensu Slaughter, 1963) is recorded from middle–late Pleistocene (late Irvingtonian–Rancholabrean) localities in North and South America. Various authors (e.g. Webb, 1974b; Robertson, 1976) have suggested interrelationships between North and South American *Smilodon*, but until now such proposals have been based on comparisons made from the literature rather than firsthand study of collections.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

Sabercats have been recorded from Argentina (Buenos Aires, and Mar del Plata and environs), Bolivia (Tarija, Ñupua), Brazil (Lagoa Santa Caves), Ecuador (La Carolina, Punin), Peru (Talara), and Uruguay (Fig. 1). The oldest record, *Smilodontidion riggii* (Kraglievich, 1948), was reported from the Chapadmalal Formation near Mar del Plata, Argentina, and assigned a Chapadmalalan (late Pliocene) age. However, according to G. Scaglia (pers. comm., 1981; Churcher, 1977:

255) this material was not collected in situ but rather from landslide deposits at the base of a cliff that are more likely Ensenadan in age.

The Uquian record of sabercats is based on material collected from the Vorohue Formation at Mar del Plata and Miramar, Argentina. According to J.L. Kraglievich's (1952) chronological subdivisions, this rock unit encompasses the Vorohuean subage, an intermediate subdivision between the Uquian and Ensenadan Land Mammal Ages, regarded by Pascual et al. (1966) as indistinguishable from the Uquian. Scaglia (pers. comm., 1981), however, questions the validity of this record and interprets this material as having been derived from Ensenadan-age deposits.

Discounting these questionable records, *Smilodon* is well documented from deposits that range in age from Ensenadan–Lujanian. Argentine localities assigned an Ensenadan age are listed by Méndez-Alzola (1941). Outside of Argentina, sabercats have been recovered from middle and late Pleistocene deposits of Tarija and Ñupua, Bolivia (Boule and Thévenin, 1920; Hoffstetter, 1963, 1968). Known collections of these faunas come from various stratigraphic levels (MacFadden et al., 1983) and are Ensenadan and possibly Lujanian in age. Lujanian age deposits that have yielded abundant *Smilodon* include Buenos Aires, and Mar del Plata and environs (Méndez-Alzola, 1941); Talara, Peru (Churcher, written comm., 1981); La Carolina and Punin, Ecuador (Hoffstetter, 1952); and various sites in Uruguay (Mones and Francis, 1973). *Smilodon* apparently became extinct in South America during the late Pleistocene; the Lujanian–Holocene Lagoa Santa Caves of Brazil represent its latest known occurrence.

SYSTEMATIC PALEONTOLOGY

Order Carnivora Bowdich, 1821

Suborder Feliformia Kretzoi, 1945

Family Felidae Gray, 1821

Subfamily Machairodontinae Gill, 1872

Tribe Smilodontini Kurtén, 1963

Genus *Smilodon* Lund, 1842

Hyaena Lund, 1839a:94 (not *Hyaena* Brisson, 1762).

Felis Lund, 1839c:271 (not *Felis* Linnaeus, 1758).

Munifelis Muñiz, 1845 (fide F. Ameghino, 1889:333).

Felis (*Trucifelis*) Leidy, 1868:175.

Trucifelis Leidy, 1869:366.

Machaerodus Lydekker, 1884:33.

Drepanodon Leidy, 1889:14.

Machairodus Leidy, 1889:14.

Machaerodus Winge, 1895:3, 13 (not *Machairodus* Kaup, 1833).

Smilodontopsis Brown, 1908:188.

Prosmilodon Rusconi, 1929:5 (as a subgenus of *Smilodon*).

Smilodontidion J.L. Kraglievich, 1948:6.

TYPE SPECIES. *Smilodon populator* Lund, 1842.

INCLUDED SPECIES. Type species and *S. gracilis* (Cope, 1880).

EMENDED DIAGNOSIS. Differs from all other machairodont genera but shares with *Megantereon* the following derived characters: glenoid process enlarged; prominent post-orbital process; well-developed supraoccipital crest; upper canines elongate, compressed and recurved; upper and lower incisors enlarged; P2/2 lost; long postcanine diastema; P3/3 reduced; P4 protocone reduced; lower canines reduced; and limbs and feet short and stocky. More derived than *Megantereon* in having incisors enlarged and procumbent; upper canines longer and more robust; P4 ectoparastyle enlarged; and mandibular flange reduced.

KNOWN DISTRIBUTION. ?Uquian. Ensenadan–Lujanian (middle–late Pleistocene) of South America and Irvingtonian–Rancholabrean (middle–late Pleistocene) of North America.

Smilodon populator Lund, 1842b

Figures 2–4

Felis cultridens Bravard, 1828:143, table III, figs. 10–13; Blainville, 1864, II (Des *Felis*, Chap. 3:141).

Hyaena neogaea Lund, 1839a:94; 1839b:224, 232; 1840a:265; 1840b:312; 1842a:12; Burmeister, 1864:123; 1879:106; Paula Couto, 1940:24; 1945:253.

Felis protopanther Lund, 1839c:207; 1840a:293, pl. XXVI, figs. 10–11; Burmeister, 1879:106; H. Gervais and F. Ameghino, 1880: (Obras II:532).

Munifelis bonaerensis Muñiz, 1845.

Machaerodus neogaeus (Lund) Pictet, 1853:221; Burmeister, 1864:123; 1867:183; 1879:106; Lydekker, 1885:47; Winge, 1895:3, 13, 80, 82; Spillman, 1931:53; 1938:373.

Felis smilodon Desmarest, 1853:150, 152, 221, 223; 1860:61; Blainville, 1855, pl. XX; Paula Couto, 1940:24; 1945:253.

Smilodon blainvillii Desmarest, 1860:61.

Felis (Trucifelis) fatalis Leidy, 1868:175.

Trucifelis fatalis Leidy, 1869.

Machaerodus necator P. Gervais, 1878:1361 (*nomen nudum*).

Machaerodus cf. *M. neogaeus* Branca, 1883:137–147, pl. XIX.

Machaerodus fatalis Lydekker, 1884:333.

Smilodon ensenadensis F. Ameghino, 1888:6 (Obras V:473); 1898:195 (Obras XII:628); Paula Couto, 1945:253, 255.

Drepanodon or *Machaerodus floridanus* Leidy, 1889:14.

Machaerodus ensenadensis F. Ameghino, 1889:339 (Obras XII:849, pl. IV, fig. 18); Bosca, 1923:182.

Smilodon floridanus Adams, 1896:433.

Smilodon crucians F. Ameghino, 1904:123 (Obras XV:201); 1909:122 (Obras XVII:610); J.L. Kraglievich, 1947:4, fig. 1.

Smilodon bonaerensis F. Ameghino, 1907:39, fig. 3 (Obras XVII:11, fig. 3); Rusconi, 1931:3, 4, 6, 8, figs. 1, 2, 4, 6, 7; Méndez-Alzola, 1941:10.

Smilodon californicus Bovard, 1907:155.

Smilodontopsis troglodytes Brown, 1908:188.

Smilodontopsis conardi Brown, 1908:190.



Figure 1. Distribution of *Smilodon populator* in South America. Symbols: ●, Lujanian; ■, Ensenadan; ○, ?Uquian.

Smilodon nebraskensis Matthew, 1918:228.

Smilodon neogaeus ensenadensis Boule and Thévenin, 1920:235, pl. XXVI, figs. 1–5.

Smilodon (Prosmilodon) ensenadensis Rusconi, 1929:5; 1936:206.

Smilodon (Trucifelis) californicus Merriam and Stock, 1932:16.

Smilodon (Trucifelis) fatalis Merriam and Stock, 1932:16.

Smilodon (Trucifelis) floridanus Merriam and Stock, 1932:16.

Smilodon (Trucifelis) nebraskensis Merriam and Stock, 1932:16.

Smilodon (Trucifelis) californicus brevipes Merriam and Stock, 1932:161.

Smilodon neogaeus Paula Couto, 1940:24–27; 1945:253, 255–256, 261, note 38; 1950:58–59, note 18, 366, note 433, 538; 1953:96, 99; Churcher, 1967:245.

Smilodon necator Paula Couto, 1940:24; 1945:253.

Smilodon (Prosmilodon) ensenadensis ferox J.L. Kraglievich, 1947:5.

Smilodon (Prosmilodon) ensenadensis minor J.L. Kraglievich, 1948:11; Rusconi, 1929:5; 1931:14.

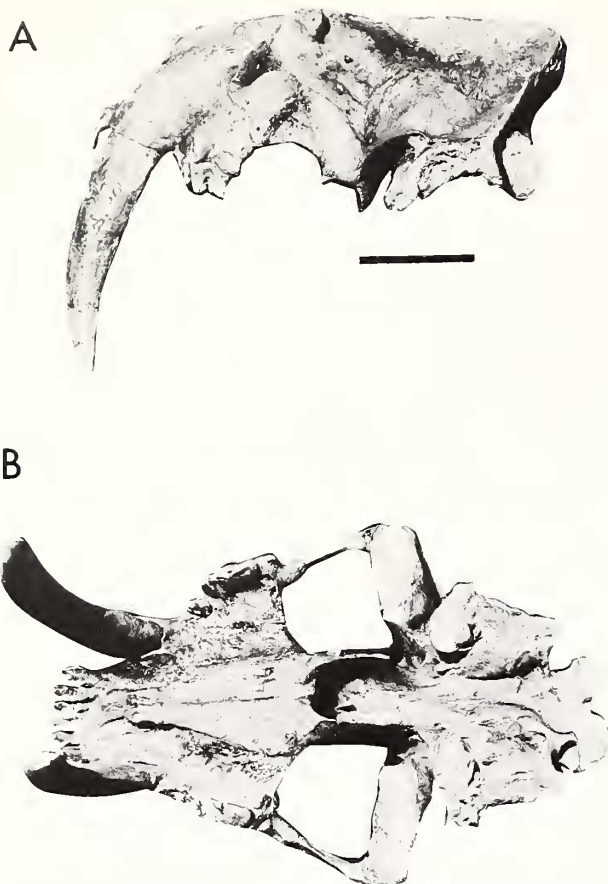


Figure 2. *Smilodon populator*, MACN 46, from near Lujan, Buenos Aires Province, Argentina. Lateral (A) and ventral (B) views of skull. Scale = 10 cm.

Smilodontidion riggii J.L. Kraglievich, 1948:6, figs. 3, 5–6, 8–9; Pascual et al., 1966:59.

Smilodon sp. Spillman, 1948:261; Hoffstetter, 1949:8; Hoffstetter, 1952:165, figs. 39, 40, pl. V, fig. 8, pl. VI, figs. 1–8.

Smilodon populator populator Paula Couto, 1955:11, fig. 10.

Smilodon trinitensis Slaughter, 1960:487.

Smilodon fatalis Slaughter, 1963:74.

SYNTYPES. UZM L specimens, right I², I³, fragmentary right C¹, left metacarpals, II, IV, and right metacarpal V; from Lagoa Santa Caves, Brazil.

Type of *S. bonaerensis*. MACN 46, a nearly complete skeleton, from Luján, Buenos Aires Province, Argentina.

Type of *S. crucians*. MACN 1460, right ramus with I₃–M₁; from Tarija, Bolivia.

Type of *S. (Prosmilodon) ensenadensis ferox*. MACN 1457, anterior portion of right ramus with symphyseal region, C root, and P_{3–4} alveoli; from Tarija, Bolivia.

Type of *S. (P.) ensenadensis minor*. MACN 16693, occipital portion of skull; MACN 16692, right cuboid; MACN 16689, right and left humeri; MACN 16695, proximal and

distal portions of left femur; MACN 16697, proximal portion of right radius; MACN 16691, proximal portion of right tibia; MACN 16690, left astragalus; right calcaneum; and MACN 16694, right metatarsal III. Probably all of the same individual; from Punta Hermengo, Miramar Province, Argentina.

Type of *Smilodontidion riggii*. MACN 6802, patella, proximal phalanges III, IV, V, femur, tibia, astragalus, calcaneum, metatarsal IV, fibula, and ischium; from Chapadmalal Formation, Buenos Aires Province, Argentina.

EMENDED DIAGNOSIS. Differs from *Smilodon gracilis* in having large, robust skull with broad muzzle, upper canines strongly recurved, upper canines and cheek teeth with finely serrated anterior and posterior margins, P⁴ with very reduced protocone, mandible usually with a single, large mental foramen, and mandibular flange greatly reduced.

SOUTH AMERICAN DISTRIBUTION. Ensenadan–Lujanian, Bolivia; Lujanian, Brazil; Lujanian, Ecuador; ?Uquian, Ensenadan–Lujanian, Argentina; Lujanian, Peru; and Lujanian, Uruguay.

SOUTH AMERICAN MATERIAL STUDIED. See Appendix 1.

DESCRIPTION

Smilodon populator is best known in North America from the late Pleistocene tar pits of Rancho La Brea, California (Merriam and Stock, 1932). The South American record of this sabercat is described herein using the Rancho La Brea sample as the standard of comparison.

SKULL. Cranial measurements are listed in Appendix 2A. South American individuals are characterized by development of very large, robustly proportioned skulls. As seen in dorsal view, the reduced nasals display deeply notched anterior ends and the muzzle is short and broad. The well inflated postorbital processes are characterized by a marked convexity of their posterior border. The zygomata are deep and widely arched (Fig. 2A). The sagittal crest rises prominently behind the slightly convex frontal region. In ventral view (Fig. 2B), the auditory bullae are slightly inflated and comparatively longer than in the Rancho La Brea sample. The enlarged mastoid process is closely appressed to the postglenoid process.

Some variation is apparent in the shape of the occiput (Fig. 3A, B). Most specimens examined show development of a rounded, convex occiput with a strong vertical keel on the basioccipital—the typical condition in *S. populator* as noted by Merriam and Stock (1932:32). However, several specimens including MACN 8682 display narrower, more triangular occiputs with less distinct vertical keels. Slaughter (1963) noted that triangular occiputs were characteristically developed among North American pre-Wisconsinan (late Irvingtonian and early Rancholabrean) *Smilodon* which he referred to *S. fatalis*. While it is generally true that most specimens that display a triangular occiput are Ensenadan or Irvingtonian in age, several Lujanian and Rancholabrean specimens (e.g. MACN 8661, Fig. 3A) also exemplify this condition. It is also possible that the shape of the occiput may represent sexual dimorphism or age variation as it was ob-

A



B

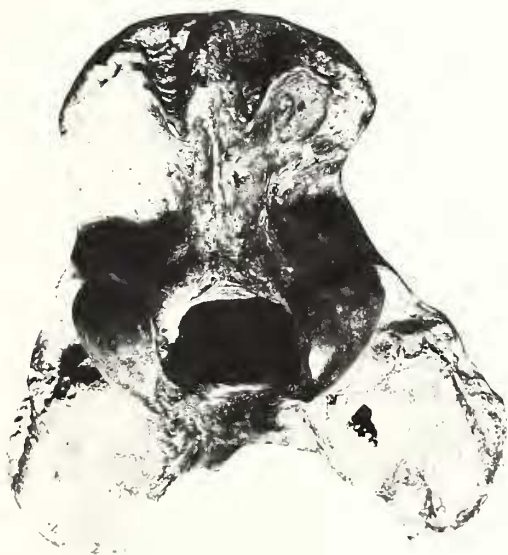


Figure 3. *Smilodon populator*, occipital views of skull showing extremes in variation. A, MACN 8661 from Olivos, Buenos Aires Province, Argentina; B, MACN 8682 from P. Piedras, Buenos Aires Province, Argentina. Scale = 10 cm.



Figure 4. *Smilodon populator*, MACN 46, from near Lujan, Buenos Aires Province, Argentina. Lateral (A) and occlusal (B) views of mandible. Scale = 5 cm.

served that those specimens that exhibit a narrower, more triangular occiput usually possess well-developed sagittal crests and often typify subadult individuals.

UPPER DENTITION. Appendix 2B lists upper tooth dimensions. Upper incisors are large, sharp and procumbent. I^1 is comprised of lingual and labial cusps positioned on either side of the V-shaped notch encircling the principal cusp. I^2 is similar in morphology, with the lingual ridge extending further anteriorly. The caniniform I^3 consists of a principal cusp and small basal cusp positioned on a circular serrate ridge on the lingual tooth margin. The strongly developed posterolateral ridge is serrated in unworn specimens.

The long, slender canine is strongly recurved and fine enamel serrations are developed on the anterior and posterior margins. Although few sabers are preserved in entirety, the canine is longer than in Rancho La Brea specimens (Fig. 2). Paula Couto (1955, table 1) lists canine length for a specimen from Brazil as approximately 277.5 mm compared with a range

of measurement for this tooth among the Rancho La Brea sample of 200–262 mm (Merriam and Stock, 1932:48).

P³ is relatively small and variable in morphology. It is double-rooted and consists of a principal cusp flanked by anterior and posterior cusps. Occasionally, a second posterior cusp develops, as in ROM 2116 and MLP 10-2. A strong anterolingual cingulum is usually present. In MACN 46, however, the anterior and posterior cusps are small, and the anterolingual cingulum is absent. The orientation of P³ varies from a linear to oblique position behind the canine.

The small ectoparastyle and parastyle of the upper carnassial form the anterior blade of the tooth. The metacone is always anteroposteriorly longer than the paracone. The protocone is usually very reduced or absent although a separate protoconal root is usually present. The occasional presence of the protocone was noted in Rancho La Brea *Smilodon* by Merriam and Stock (1932:48) and confirmed in this study. Unworn specimens characteristically show development of serrations along the cutting edge. M¹ is a very reduced, double-rooted tooth with a transversely elongated crown comprised of a principal cusp, the parametacone, and a small protocone. The tooth is oriented at nearly right angles to the anteroposterior axis of P⁴.

MANDIBLE. The horizontal ramus is anteroposteriorly short and robust (Fig. 4A, B, Appendix 2A). The anterior face of the massive symphysis is concave and pitted by foramina. The flange is very reduced ventrally in comparison with *Smilodon gracilis*, although its anterior margin is usually thick and laterally flared. The diastema between the C and P₄ is comparatively shorter among most of the South American sample although its length is variable, a feature apparently related to age (Merriam and Stock, 1932, pl. 4). Usually a single, large mental foramen is positioned below the diastema near the ventral border of the ramus although double foramina occasionally occur in the Californian and Talaran populations (Churcher, 1984; this study). The coronoid process is greatly reduced. Among several South American specimens (e.g. MACN 46 and MACN 18057) the prominent angular process swings laterally farther away from the deeply excavated masseteric fossa than in most Rancholabrean specimens (Fig. 4).

LOWER DENTITION. Appendix 2B lists lower tooth dimensions. Lower incisors are broad, recurved, and set in a transverse line. The small I₁ bears a prominent V-shaped notch encircling the principal cusp and a lingual ridge which terminates in a basal cusp. I₂ is similar in morphology, with serrations present on the lingual ridge. The caniniform I₃ exhibits a prominent serrate lingual ridge. The lower canine has in addition to the lingual ridge a prominent posterior ridge, slightly labial to the midline of the tooth; both ridges are serrated.

P₃, commonly present in Ensenadan and Irvingtonian specimens, is extremely variable in morphology (CV for length = 23.4). In MACN 6270, P₃ is single-rooted and comprised of a single principal cusp followed by a small posterior cusp. In another specimen, ROM 5100, the alveolus for this tooth indicates that it was double-rooted. Loss of P₃ is more common among Lujanian and Rancholabrean specimens. As

noted by Merriam and Stock (1932:51), this tooth is present in only 6% of the La Brea sample (N = 678).

P₄ is double-rooted and comprised of a principal cusp flanked by a relatively small anterior cusp and two progressively smaller posterior cusps. The second posterior cusp is occasionally positioned on a strong lingual cingulum. The crown of this tooth and M₁ are inclined posteriorly.

M₁ usually possesses a small anterior cingulum in front of the paraconid. Presence of this cusp among North American specimens was previously noted (Bovard, 1907). The paraconid blade is noticeably shorter anteroposteriorly than the protoconid and both are serrated. Most specimens show slight development of a basal posterior cingulum behind the protoconid.

DISCUSSION

The known South American samples of sabercats are all referred to *Smilodon populator*. As previously mentioned, *Smilodon* was established by Lund (1842b) who described a single species, *S. populator*, from the Lagoa Santa Caves, Brazil. Muñiz (1845) described a sabercat skeleton collected from near Luján, Argentina, under the name *Munifelis bonaerensis*. However, his generic name is invalid since it was published in a newspaper (La Gaceta Mercantil), which does not satisfy the publication requirement established by the International Code of Zoological Nomenclature. Later authors (Ameghino, 1907; Rusconi, 1931; Méndez-Alzola, 1941) incorrectly referred to sabercats under the name *Smilodon bonaerensis*. Burmeister (1867) applied the name *Machaerodus bonaerensis* to the Argentine material, although he later acknowledged that *S. bonaerensis* was probably conspecific with *S. neogaeus* (Lund, 1839a).

Ameghino (1888:6) described *Smilodon ensenadensis* (= *Machaerodus ensenadensis*) based on an upper canine recovered from Ensenadan deposits in Ensenada, Argentina. Rusconi (1929) listed small sabercats from the Ensenadan of Argentina under the subgenus *Smilodon* (*Prosmilodon*). L. Kraglievich (1934) followed Rusconi's usage of *Prosmilodon*. In 1947 J.L. Kraglievich formally diagnosed *Smilodon* (*Prosmilodon*) on the basis of its small size and presence of P₃. The variable presence of this tooth among smilodontines has been previously discussed. Presence or absence of this tooth generally can be used to distinguish Ensenadan or Irvingtonian *S. populator* from Lujanian or Rancholabrean forms of this species.

A right ramus (MACN 1457) collected from Tarija, Bolivia, and originally described and figured by Ameghino (1902) as *Machaerodus ensenadensis*, was referred by Kraglievich (1947) to *Smilodon* (*Prosmilodon*) *ensenadensis ferox*. This subspecies was distinguished from *S. bonaerensis* on the basis of its smaller size, lack of serrations on the upper canine, and presence of a double-rooted P₃. Examination of the type and referred material indicates that the upper canine is heavily worn along both the anterior and posterior margins, obliterating serrations had they been present. A second subspecies, *Smilodon* (*Prosmilodon*) *ensenadensis minor*, was distinguished by J.L. Kraglievich (1948) on the basis of its

Table 1A. ANCOVA for length of lower canine of *Smilodon populator* adjusted for length and width of P_4 as a test for significant differences based on locality and age. * = $P \leq 0.05$, ** = $P < 0.01$. Abbreviations = AP = anteroposterior length, T = transverse width.

Souce of variation	Sum of squares	Degrees of freedom	Mean square	F-value	Regression coefficient
Locality	0.06274	1	0.06274	0.04	
Age	37.41456	1	37.41456	23.32**	
Locality/age	29.88608	1	29.88608	18.63**	
AP, P_4	6.25910	1	6.25910	3.90*	0.23330
T, P_4	0.00007	1	0.00007	0.00	-0.00183
AP & T, P_4	12.34655	2	6.17328	3.85*	
Error	75.41120	47	1.60449		

smaller size and more robust postcranium. Examination of the type indicates that it falls within the limits of variation shown by *Smilodon*. The subgenus *Smilodon* (*Prosmilodon*) is here referred to *Smilodon*.

Smilodon crucians was recognized by Ameghino (1904) on the basis of its small size, shallow ramus, and long postcanine diastema. These characters are attributable to ontogenetic variation (see Merriam and Stock, 1932, pl. 4, fig. 10) and indicate that *S. crucians* represents a juvenile individual. As expected, the high coefficient of variation value for postcanine diastema length among both North and South American sabercats (see Appendix 2A) further weakens its use as a taxonomic character. Examination of the holotype of *S. crucians* (MACN 1460) revealed the presence of serrations on the lower canine and cheek teeth, which supports synonymy of this species with *S. populator*.

A new genus of sabercat, *Smilodontidion*, was proposed by J.L. Kraglievich (1948) on the basis of limb elements collected from near Chapadmalal, Argentina. This genus was distinguished by its smaller size and slightly different morphology, regarded here as the result of both individual and age variation. The incomplete fusion of epiphyses on the femur and tibia indicates that this specimen represents a young adult. I agree with Churcher (1967) that *Smilodontidion* should be synonymized with *Smilodon*.

The results of systematic reevaluation of North American *Smilodon* are summarized in the following discussion (see also Berta, in press). The oldest name for a North American *Smilodon* is *Felis* (*Trucifelis*) *fatalis* proposed by Leidy (1868). The type, a fragmentary maxilla containing P^4 from Hardin County, Texas, redescribed and illustrated by Leidy (1869) is judged too incomplete to provide specific diagnosis. Later, Leidy (1889) described a fragmentary skull lacking teeth as a new species of the European genus *Machairodus*, *M. floridanus*. This species has been referred to *Smilodon* by all later workers. Bovard (1907) proposed the species of *Smilodon californicus* separating it from *S. floridanus* by the

Table 1B. Adjusted group means for length of lower canine of *Smilodon populator*. Abbreviations: N = sample size, as in Table 1A.

	North America		South America	
Age	Rancholabrean	Irvingtonian	Lujanian	Ensenadan
AP, C	14.81744	13.80000	17.81667	11.43333
N	43	4	3	3

latter's shorter muzzle, more posterior position of the posterior nares and possibly by ridges on the palate. The sample from Rancho La Brea consisting of thousands of individuals was more fully described by Merriam and Stock (1932) who proposed certain differences in the mastoid region to distinguish the two species. Kurtén's (1965) study of Florida sabercats led him to synonymize *S. floridanus* with *S. fatalis* and maintain *S. californicus* as distinct. Webb (1974b) in his evaluation of additional Florida material strengthened the case for synonymy of *S. californicus* with *S. floridanus* using broad overlap of cranial, mandibular, and tooth measurements.

More recently, Kurtén and Anderson (1980) recognized a single derived species, *Smilodon fatalis* and considered "the numerous North American taxa of sabertooths (with the exception of *S. gracilis*) to have, at most, subspecific standing." Churcher (1984) followed Slaughter (1963) in assigning to *Smilodon fatalis* the following species: *Smilodontopsis conardi* Brown, 1908; *Smilodontopsis troglodytes* Brown, 1908; *Smilodon nebraskensis* Matthew, 1918; and *Smilodon trinitensis* Slaughter (1960).

The genus *Smilodontopsis* proposed by Brown (1908) was founded on specimens from the Conard Fissure, Arkansas, and distinguished from *Smilodon* by the possession of an entepicondylar foramen on the humerus. Two species, *S. troglodytes* and *S. conardi* were described on differences in the morphology of the upper carnassial. *Smilodon nebraskensis* was based on a lower jaw from Nebraska and distinguished from *S. californicus* by its "decidedly shorter postcanine diastema" (Matthew, 1918), a character of suspect taxonomic value. *Smilodon trinitensis* was founded by Slaughter (1960) on a lower jaw from the Trinity River, at Dallas, Texas. It was distinguished from previously described species by its large cheek teeth, relative to mandibular measurements and the absence of P_3 . As noted previously, P_3 is more commonly present in middle Pleistocene samples and is extremely variable in morphology.

The taxonomic confusion surrounding North American *Smilodon* brought out in the preceding discussion suggested as the next step, critical evaluation of the status of *S. floridanus* and *S. fatalis* (sensu Slaughter, 1963). As shown in this study, all of the characters diagnostic of North American *S. floridanus* also typify South American *S. populator*. Among the most useful of these characters are: large, robust skull with broad muzzle, upper canines strongly recurved, upper canines and cheek teeth with finely serrated margins, P^4 with

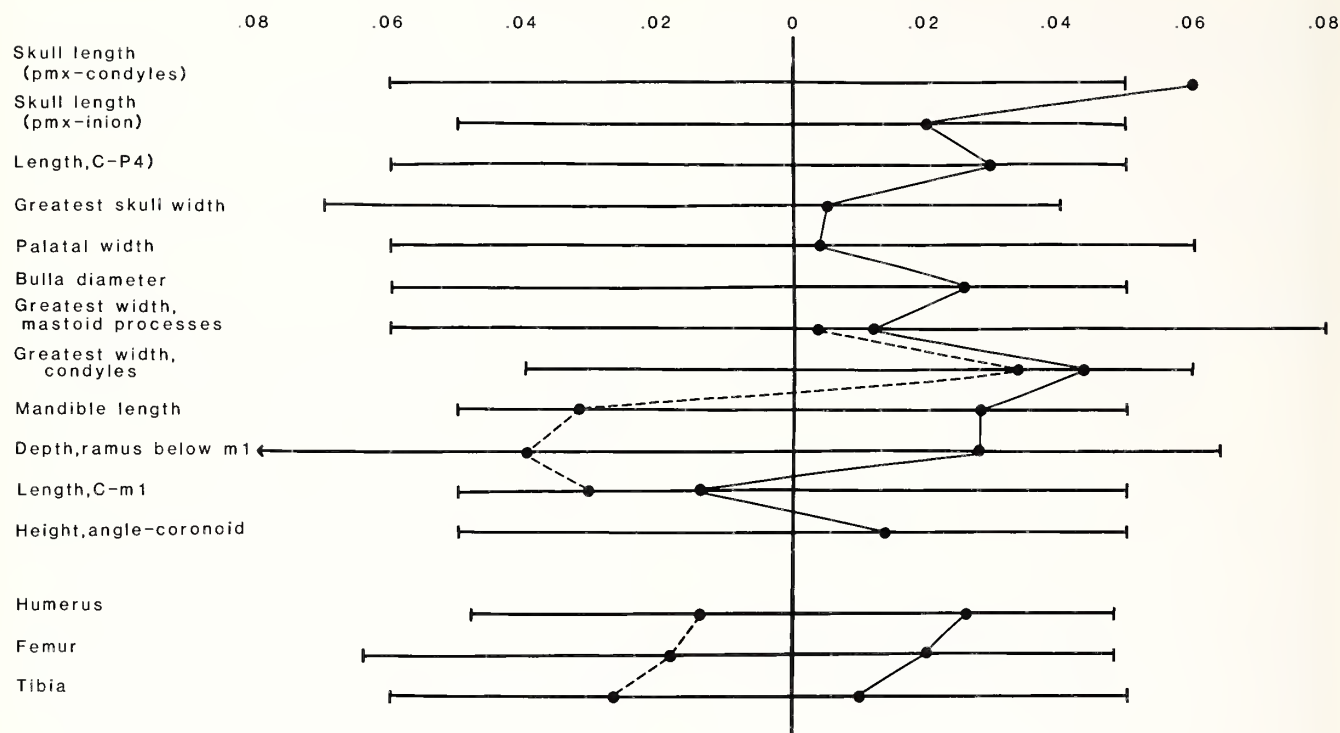


Figure 5. Ratio diagram of cranial, mandibular, tooth, and limb measurements (see Appendix 2) of South American *Smilodon populator* (solid line, Lujanian sample; dashed line, Ensenadan sample) compared with North American *Smilodon populator* (Rancho La Brea sample; Merriam and Stock, 1932) as the standard. A log difference scale is provided and horizontal bars show the observed range of variation of the standard.

very reduced protocone, mandible usually with a single, large mental foramen, and mandibular flange greatly reduced.

A ratio diagram (Fig. 5 see Appendix 2 for sample statistics; for the method see Simpson, 1941) illustrates the differences between mean measurements of South American *S. populator* and the Rancho La Brea sample, the standard of comparison. Two sets of data are compared: (1) skull and mandible dimensions and (2) forelimb and hindlimb lengths from both North and South American middle and late Pleistocene samples. South American specimens of *S. populator* from late Pleistocene (Lujanian) localities are on the average larger for nearly every dimension studied than North American Rancho La Brea individuals, an observation noted previously by Paula Couto (1955) and Kurtén (1965). However, nearly all of the South American specimens fall within the observed range of variation for the Rancho La Brea sample.

Although sample sizes are small, mandibular dimensions of middle Pleistocene (Ensenadan) *S. populator* average smaller than either Lujanian or Rancholabrean specimens. Mean values of lower tooth dimensions for South American *S. populator* from Ensenadan localities approximate those of North American Irvingtonian individuals with several exceptions. Among Ensenadan individuals P_3 averages larger whereas P_4 and M_1 average smaller than corresponding teeth in Irvingtonian specimens (Appendix 2B).

While most limb elements are short and stocky in smilodontines, this is not true for the femur of *S. populator* which is proportionately longer and not nearly as robust as in most large felids (Gonyea, 1976, table 4, fig. 6). Analysis of limb lengths (Appendix 2C, Fig. 5) suggest that the principal fore- and hindlimb elements (humerus, femur, and tibia) average longer among Lujanian *S. populator* than the same elements among Rancholabrean individuals. Proportions of the hindlimb of Ensenadan *S. populator* are much the same as the Rancholabrean population except for their smaller size.

Slaughter (1963) used five characters to diagnose *S. fatalis*. Each of these characters is listed below and then reconsidered in light of reexamination of both North and South American specimens.

(1) Total skull length less than any specimen of *S. californicus* (= *S. floridanus*). Following Merriam and Stock (1932), Slaughter (1963, table 3) lists the smallest skull from Rancho La Brea as 256.4 mm. Although the present study substantiates this claim, six skulls ranging between 259.5 and 273.0 mm increase the previously known North American sample of "small" *S. populator* individuals.

(2) Occiput narrow and triangular, not rounded above. As previously discussed, occiput shape is variable. North and South American populations of middle and late Pleistocene *S. populator* contain specimens which exhibit narrow, tri-

angular occiputs although they are more common among middle Pleistocene individuals.

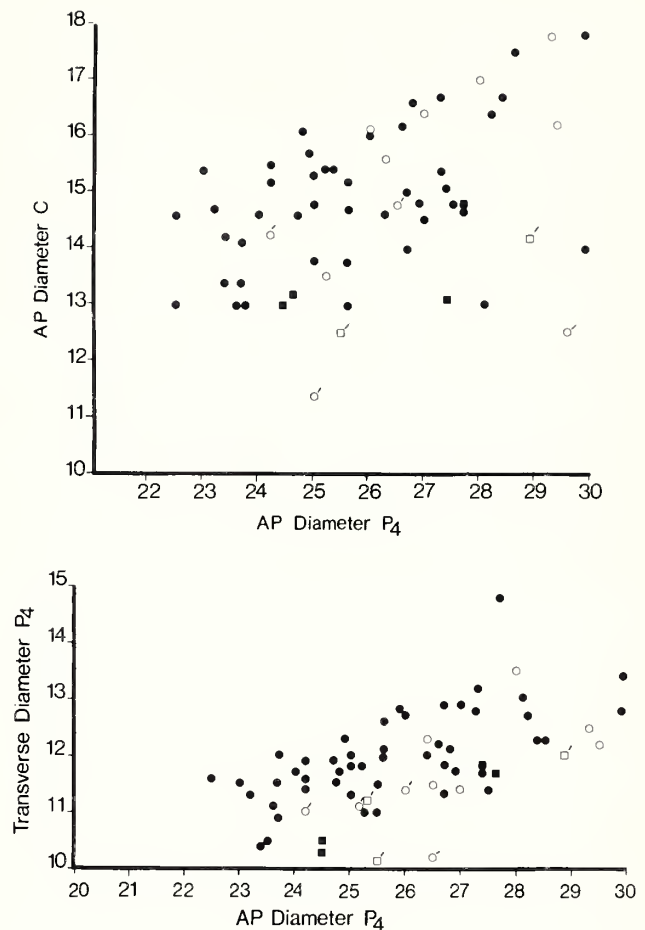
(3) Basioccipital lacking well-developed keel. This was the most variable character observed. Although it is often associated with a more triangular occiput, just as many individuals with a rounded occiput display an indistinct, flattened keel.

(4) Inferior canine much reduced with anteroposterior diameter less than 54% of the same measurement of P^4 .

(5) P^4 thin, having a transverse diameter less than 43% of the anteroposterior diameter. In his figures 1 and 2 Slaughter showed a difference between North American *Smilodon californicus* material of late Pleistocene (Wisconsin) age from California and Florida and a smaller group of all middle Pleistocene (pre-Wisconsin) material which he referred to *Smilodon fatalis*. Figure 6 presented here repeats Slaughter's bivariate plots with the addition of South American *Smilodon populator*. When these data are added the ranges of the various measurements overlap and strengthen the case for synonymy of North American *Smilodon* species with South American *Smilodon populator*.

Slaughter's dental characters (length of lower canine adjusted for length and width of P_4) were further evaluated in an analysis of covariance (ANCOVA) for *Smilodon populator* collected from (1) different localities (North vs. South America) and (2) different ages (middle vs. late Pleistocene) (Table 1A and B). Mean length of canine for *S. populator* differed only in age within the South American sample which led to the significant interaction term (Table 1B). However, for the characters evaluated sample sizes for middle Pleistocene *Smilodon* are very small ($N = 4$, North America; $N = 3$, South America). When age is eliminated as a factor and P_4 length is adjusted for width, using a pooled late Pleistocene sample there is no significant difference in adjusted means between North and South American *S. populator* (adjusted group means for length of P_4 ; North American samples = 39.74772, South American samples = 41.48333). The results of analysis of covariance using Slaughter's dental characters do not support recognition of more than one *Smilodon* species; both North and South American samples are referred to *S. populator*.

The practice of recognizing a species solely on the basis of size is questioned here for several reasons. Earlier work (Slaughter, 1963; Webb, 1974b) has shown that size overlap in a number of cranial and tooth measurements for *Smilodon* is too great to permit species discrimination. Size variation has been previously identified among wide-ranging large carnivores; the spotted hyena (*Crocuta crocuta*) (Kurtén, 1957) and the puma (*Felis concolor*) (Kurtén, 1973). Strong sexual dimorphism in the puma was demonstrated for all skull and tooth measurements studied (condylobasal length, zygomatic width, C length, P^4 length, and M_1 length). The results of comparison of these variances in a standardized local population of North American *Felis concolor* statistically adjusted for 35°N latitude (Kurtén, 1973; table 2) and in the combined North and South American *Smilodon populator* are given in Table 2. Statistically significant differences were



Figures 6A, 6B. Fig. 6A. Bivariate plot of canine length versus P_4 length for *Smilodon populator* and *Smilodon fatalis* (sensu Slaughter, 1963). Plot gives comparison of *S. populator* from North America (data from Merriam and Stock, 1932 and this study; ●, Rancholabrean) and South America (data from this study; ○, Lujanian, □, Ensenadan), and *Smilodon fatalis* from North America (data from Slaughter, 1963; ■, Rancholabrean, □, Irvingtonian). Fig. 6B. Bivariate plot of P_4 width versus length for *Smilodon populator* and *Smilodon fatalis* (sensu Slaughter, 1963). Comparison and symbols as above.

observed between these variances for only two dimensions, condylobasal length and zygomatic width. If one assumes a similar pattern of variation among other large cats then greater importance can be attached to the fact that all other dimensions (C, P^4 , and M_1 lengths) do not show any statistically significant differences between samples. The data indicate that for these tooth dimensions, variation in *S. populator* can be accounted for simply as the result of sexual dimorphism. Kurtén was able to distinguish sexual variation from individual and latitudinal variation in the puma. In the present study comparisons were made on the basis of total variability within *S. populator* since I could not partition the variances associated with either sex or latitude. Based on Kurtén's data,

Table 2. Variation in *Felis concolor*¹ and *Smilodon populator* from North and South America. Abbreviations: N = sample size; s² = variance; F = F ratio; P = probability; 1 = data from Kurtén, 1973, table 2.

Character	N	Taxon	s ²	F	P
Condylobasal length	116	<i>F. concolor</i>	163.890	1.928	~0.02
	28	<i>S. populator</i>	316.008		
Zygomatic width	118	<i>F. concolor</i>	115.313	8.170	~0.001
	30	<i>S. populator</i>	14.113		
C length	144	<i>F. concolor</i>	1.507	1.435	~0.2
	37	<i>S. populator</i>	2.164		
P ⁴ length	141	<i>F. concolor</i>	0.649	1.200	~0.5
	31	<i>S. populator</i>	0.79		
M ₁ length	143	<i>F. concolor</i>	0.268	1.06	~0.5
	42	<i>S. populator</i>	0.252		

undoubtedly, both individual and latitudinal variation are important aspects to the observed variation in *Smilodon*. However, the fact that the comparable variation in tooth dimensions in North and South American *Smilodon* can be accounted for solely by sexual dimorphism without consideration of these other parameters, further strengthens the argument for recognition of *Smilodon populator* as a single wide-ranging species.

PHYLOGENETIC RELATIONSHIPS AND ZOOGEOGRAPHIC PATTERNS

Judging from the oldest stratigraphic record, sabercats of the genus *Smilodon* originated in North America during the late Cenozoic. *S. gracilis* (Cope, 1880), the sister taxon of the more derived *S. populator*, is well represented from the late Blancan through Irvingtonian of Florida. This species is also known from the type locality at Port Kennedy Cave in Pennsylvania and with less certainty from the Palm Springs Formation, Vallecito Creek, California (Kurtén and Anderson, 1980; Berta, in press). The following characters distinguish *S. gracilis* from *S. populator*: canines only slightly recurved; canines and cheek teeth with very finely serrated margins; P⁴ with well-developed protocone; mandible with two mental foramina and an enlarged flange (Berta, in press).

The earliest record of *S. populator* is from the Irvingtonian of Arkansas, California, and Nebraska. During the late Pleistocene *S. populator* extended its range throughout the United States, Central America, and into South America. In South America, this species has been recorded from Argentina, Bolivia, Brazil, Peru, and Uruguay. The extension of *S. populator* into South America is not so surprising when one considers the equally wide range of such present-day species as the lion, *Felis leo* and the puma, *Felis concolor*.

The end of the Pleistocene marked the extinction of *Smilodon* in both North and South America. As was true for large canids the extinction of sabercats can be related to extinction of their large, thick-skinned herbivorous prey which

included ground sloths, glyptodonts, proboscideans, horses, notoungulates, and litopterns. While supporting this interpretation of *Smilodon* prey, Akersten (1985) added that the "canine shear-bite" of this species would have been just as effective on smaller thin-skinned prey. However, it should be stressed, as elaborated by Rosenzweig (1966), that larger carnivores generally take larger prey. It seems likely that the extinction of sabercats can be related in part to their specialized hunting and feeding strategy and resultant social behavior which was dependent on a large herbivore megafauna, so reduced in number and diversity at the present time.

ACKNOWLEDGMENTS

Much of this research was undertaken at the Vertebrate Paleontology Section of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires (MACN), where José Bonaparte (Chief of Section of Fossil Vertebrates) made collections, working space, and library facilities available. Rosendo Pascual and Guiomar Vucetich, Facultad de Ciencias Naturales y Museo de la Universidad Nacional de La Plata (MLP), and Galileo J. Scaglia, Director, Museo Municipal de Ciencias Naturales, Mar del Plata (MMP), gave permission to study collections under their care and facilitated research in many ways. David Wright measured specimens in the University of Nebraska collections. D.A. Farris assisted with statistical manipulation of the data. W. Akersten, H. Galiano, E. Manning, B.J. MacFadden, L. Marcus, C.A. Repenning, R.G. Wolff, and S.D. Webb critically reviewed this manuscript.

Financial support from Sigma Xi, the Hays Fund of the American Philosophical Society, Thomas J. Dee Research Fellowship (Field Museum of Natural History, Chicago), the Department of Natural Sciences, Florida State Museum, University of Florida is gratefully acknowledged. This research was initiated during tenure of a Postdoctoral Fellowship at the Department of Natural Sciences, Florida State Museum, University of Florida. This report is University of Florida Contribution to Vertebrate Paleontology number 214.

LITERATURE CITED

- Adams, G.I. 1896. The extinct Felidae of North America. American Journal of Science, Ser. 4, 1:419-444.
- Akersten, W.A. 1985. Canine function in *Smilodon* (Mammalia; Felidae; Machairodontinae). Contributions in Science, 356, Natural History Museum of Los Angeles County, 1-22.
- Ameghino, F. 1888. Rápidas diagnosis de algunos mamíferos fósiles nuevos de la República Argentina. Buenos Aires, 17 pp. (Ameghino Obras V:471-480).
- . 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina, obra escrita bajo los auspicios de la Academia nacional de Ciencias de la Republica Argentina para presentarla a la Exposición Universal de Paris de 1889. Actas de la Academia Nacional de Ciencias, Córdoba, VI:xxxiii + 1027 pp. (Ameghino Obras VI-IX).
- . 1898. Sinopsis geológico-paleontológica. Segundo

- censo de la Republica Argentina. Fol., Buenos Aires, 1: 112–255 (Ameghino Obras XII:487–734).
- . 1902. Notas sobre algunos mamíferos fósiles nuevos ó poco conocidos del valle de Tarijá. *Anales del Museo nacional de historia natural*, Buenos Aires 3(1): 225–261 (Ameghino Obras XIII:837–867).
- . 1904. Nuevas especies de mamíferos cretáceos y terciarios de la República Argentina. *Anales de la Sociedad científica Argentina* 56, 57, 58:1–142 (Ameghino Obras XV:95–218).
- . 1907. Sobre dos esqueletos de mamíferos fósiles armados recientemente en el Museo Nacional. *Anales del Museo nacional de historia natural*, Buenos Aires (3) 9:35–43 (Ameghino Obras XVII:5–14).
- . 1909. El *Diprothomo platensis*: un precursor del hombre del Plioceno inferior de Buenos Aires. *Anales del Museo nacional de historia natural*, Buenos Aires (3) 12:107–209 (Ameghino Obras XVII:592–707).
- Berta, A. in press. The sabercat, *Smilodon gracilis* from Florida and a discussion of its relationships (Felidae, Machairodontinae, Smilodontini). *Bulletin of the Florida State Museum, Biological Sciences*.
- Blainville, H.M.D. de. 1839–1864. *Ostéographie ou description iconographique comparée du squelette et du système dentaire des mammifères récent et fossile pour servir de base à la zoologie et à la géologie*. 4 vols., Paris.
- Bosca, E. 1923. Notas sobre el esqueleto inédito de *Machaerodus ensenadensis* Ameghino. Fósil del la formación pampeana (Argentina). *Boletín de la R. Sociedad española de historia natural* 23:182–188.
- Boule, M., and A. Thevenin. 1920. Mammifères fossiles de Tarija. *Miss. Sci. Crequi. Montfort et E.S. de la Grange. Soudier*, Paris, 255 pp.
- Bovard, J.F. 1907. Notes on Quaternary Felidae from California. University of California Publication, *Bulletin of the Department of Geology* 5:155–170.
- Branca, W. von. 1883. Eine fossile Säugethier-Fauna von Punin bei Riobamba in Ecuador. *Geologische und paläontologische Abhandlungen* 1(2):19–160.
- Bravard, A. 1828. *Monographie de la Montagne de Perrier près d'Issoire (Puy-de-Dôme) et deux espèces fossiles du genre Felis, découvertes dans l'une de ses couches d'alluvion*. Paris, 147 pp.
- Brisson, M.J. 1762. *Regnum animale in classes IX distributum sive synopsis methodica*. Editio altera auctior. Theodorum Haak, Leiden, 296 pp.
- Brown, B. 1908. The Conard Fissure, a Pleistocene bone deposit in northern Arkansas: with descriptions of two new genera and twenty new species of mammals. *Memoirs of the American Museum of Natural History* 9:158–208.
- Burmeister, H. 1864. Fauna Argentina. I. Mamíferos fósiles. *Anales del Museo nacional de historia natural*, Buenos Aires 1:123–142.
- . 1867. Bericht über ein Skelet von *Machaerodus*, im Staats-Museum zu Buenos Aires. *Abhandlungen der naturforschenden Gesellschaft, Halle X*:181–196.
- . 1879. Description physique de la République Argentine d'après des observations personnelles et étrangères. Traduit d'allemand avec le concours de E. Dai-reaux. Tome troisième: Animaux vertébrés. Première partie: Mammifères vivants et éteints. Buenos Aires, 3(1):1–556.
- Churcher, C.S. 1967. *Smilodon neogaeus* en las barrancas costeras de Mar del Plata, Provincia de Buenos Aires. *Publicaciones del Museo Municipal de Ciencias Naturales de Mar del Plata* 1(8):245–262.
- . 1984. The status of *Smilodontopsis* (Brown, 1908) and *Ischyrosmilus* (Merriam, 1918). *Life Sciences Contribution* 140, Royal Ontario Museum, Toronto, 59 pp.
- Cope, E.D. 1880. On the extinct cats of America. *American Naturalist* 14:833–858.
- Desmarest, E. 1853. Carnassiers. In *Chenu Encyclopédie d'Histoire Naturelle*, Carnassiers, 2e, part:222–224, fig. 102, Paris.
- . 1860. Notions générales sur la Zoologie et la Phytologie, Minéralogie, Géologie, Races humaines. In *Chenu Encyclopédie d'Histoire Naturelle*, Carnassiers, 2e, part:61, Paris.
- Dixon, W.J., and M.B. Brown. 1979. BMDP-79: Biomedical computer programs P-series. Berkeley, Univ. California Press, 880 pp.
- Gervais, H., and F. Ameghino. 1880. Les mammifères fossiles de l'Amérique du Sud. Buenos Aires and Paris, xi + 225 pp. (Ameghino Obras II:512–645).
- Gervais, P. 1878. Nouvelles recherches sur les Mammifères fossiles propres à l'Amérique méridionale. *Comptes rendus hebdomadaires des séances de l'Académie des sciences*, Paris 86(22):1359–1362.
- Gonyea, W.D. 1976. Behavioral implications of saber-toothed felid morphology. *Paleobiology* 2:332–342.
- Hoffstetter, R.H. 1949. Les félins du Pléistocène de l'Equateur. I. Faune actuelle et méthode de comparaison. *Travaux Institut France Etudes Andines* 1:3–53.
- . 1952. Les mammifères Pléistocènes de la République de l'Equateur. *Mémoires de la Société géologique de France*, Paris (n.s.) 31(66):1–391.
- . 1963. La faune Pléistocène de Tarija (Bolivia). Note préliminaire. *Bulletin du Muséum (national) d'histoire naturelle*, Paris, ser. 2, 35(2):194–203.
- . 1968. Ñuapua, un gisement de vertébrés Pléistocène dans le chaco bolivien. *Bulletin du Muséum (national) d'histoire naturelle*, Paris 40:823–836.
- Kraglievich, J.L. 1947. Sobre el tipo de *Smilodon crucians* Ameghino. *Comunicaciones, Museo Argentino de Ciencias Naturales* 1(3):1–6.
- . 1948. *Smilodontidion riggii*, n. gen., n. sp.: un nuevo pequeño esmilodonte en la fauna Pliocena de Chapadmalal. *Revista del Museo Argentino de Ciencias Naturales*, “Bernardino Rivadavia,” *Ciencias Zoológica* 1:1–44.
- . 1952. Un cánido del Eocuaternario de Mar del Plata y sus relaciones con otras formas brasileñas y norteamericanas. *Revista del Museo Municipal de Ciencias Naturales y Tradicional de Mar del Plata* 1:53–70.
- Kraglievich, L. 1934. La antigüedad pliocena de las faunas

- de Monte Hermoso y Chapadmalal, deducidas de su comparación con las que le precedieron y sucedieron. El Siglo Ilustrado No. 938:1-136; Montevideo.
- Kurtén, B.J. 1957. The bears and hyenas of the interglacials. *Quaternaria* 4:69-81.
- . 1965. The Pleistocene Felidae of Florida. *Bulletin of the Florida State Museum, Biological Sciences* 9:215-273.
- . 1973. Geographic variation in size in the Puma (*Felis concolor*). *Commentationes Biologiae* 63:1-8.
- Kurtén, B.J., and E. Anderson. 1980. Pleistocene mammals of North America. Columbia Univ. Press, New York, 442 pp.
- Leidy, J. 1868. Notice of some vertebrate remains from Hardin County, Texas. *Proceedings of the Academy of Natural Sciences of Philadelphia for 1868*:174-176.
- . 1869. The extinct mammalian fauna of Dakota and Nebraska, etc. *Journal of the Academy of Natural Sciences of Philadelphia, Ser. 2*, 7:1-VIII, 8-472.
- . 1889. The sabre-tooth tiger of Florida. *Proceedings of the Academy of Natural Sciences of Philadelphia for 1889*:29-31.
- Lund, P.W. 1839a. Blik paa Brasiliens dyreverden för sidste jordamvæltning. Anden Afh. Pattedyrene. Lagoa Santa, d. 16 Nov., 1837. *Danske videnskabernes Selskabs naturvidenskabelige og matematiske Afhandlingar VIII*: 61-144. (Portuguese transl. Lund, P.W. 1950, Chapter IV:131-203).
- . 1839b. Coup d'oeil sur les espèces éteintes de Mammifères du Brésil; extrait de quelques mémoires présentés à l'Académie royale de Copenhague. *Annales des sciences naturelles (Paris)*, (2) XI:214-234. (Portuguese transl. Lund, P.W. 1950, Chapter VI:251-269.)
- . 1839c. Nouvelles observations sur la faune fossile du Brésil, extraits d'une lettre adressée aux rédacteurs par M. Lund. *Annales des sciences naturelles (Paris)*, (2) XII:205-208. (Portuguese transl. Lund, P.W. 1950, Chapter VI:269-272.)
- . 1840a. Tillaeg til de to Sidste Afhandlingar over Brasiliens Dyreverden för sidste jordamvæltning. Lagoa Santa d. 4 April 1839. Copenhague.—K. Danske videnskabernes Selskabs naturvidenskabelige og matematiske Afhandlingar VIII:274-296, pls. XIV-XXVI. (Portuguese transl. Lund, P.W. 1950, Chapter VII:273-292.)
- . 1840b. Nouvelles recherches sur la faune fossile du Brésil. *Annales des sciences naturelles (Paris)*, (2) XIII: 310-319. (Portuguese transl. Lund, P.W. 1950, Chapter IX:307-316.)
- . 1842a. Fortsatte Bemaerkninger over Brasiliens Uddode Dyrskabning. Lagoa Santa d. 27 marts 1840. Copenhague.—K. Danske videnskabernes Selskabs naturvidenskabelige og matematiske Afhandlingar IX: 122-136. (Portuguese transl. Lund, P.W. 1950, Chapter VIII:292-305.)
- . 1842b. Blik paa Brasiliens Dyreverden för sidste Jordamvæltning. Fjerde Afhandling: Fortsaettelse af Pattedyrene. Lagoa Santa d 30 Januar. 1841. Copenhague.—K. Danske videnskabernes Selskabs naturvidenskabelige og matematiske Afhandlingar IX:137-208. (Portuguese transl. Lund, P.W. 1950, Chapter X:317-377.)
- . 1842c. Carta escripta da Lagôa Santa (Minas Geraes) ao Sr. 1º Seerretario do Instituto, pelo socio honorario Sr. Dr. Lund. *Revista trimensal de historia e geographia, ou Journal do Instituto historico e geographico Brasileiro, Rio de Janeiro IV*:80-87.
- . 1843. Blik paa Brasiliens Dyreverden för sidste jordamvæltning. Fjerde Afhandling: Om de nulevende og uddode arter af Rovdyrenes Families. Lagoa Santa d. 4 October 1841. Copenhague.—K. Danske videnskabernes Selskabs naturvidenskabelige og matematiske Afhandlingar XI:4-82, Pls. XL-XLVI. (Portuguese transl. Lund, P.W. 1950, Chapter XI:381-455.)
- . 1844. Carta do Dr. Lund, escripta da Lagôa Santa (Minas Geraes a 21 de abril de 1844). *Revista trimensal de historia e geographis, ou Journal do Instituto historico e geographico Brasileiro, Rio de Janeiro VI*:334-342. (Portuguese transl. Lund, P.W. 1950:489-498.)
- . 1845. Modellele af Det Udbytte De: 1844 Undersøgte Knoglohuler have Argivet til Kundskaben om Brasiliens Dyreverden för sidste jordamvæltning. Lagoa Santa d. 22 Nov. 1844. Copenhague.—K. Danske videnskabernes Selskabs naturvidenskabelige og matematiske Afhandlingar XII:60-94. (Portuguese transl. Lund, P.W. 1950, Chapter XVI:505-548.)
- . 1950. *Mémorias sobre a paleontologia Brasileira* *Revistas e comentadas por Carlos de Paula Couto*. Rio de Janeiro: Ministerio de Educação e Saude Instituto Nacional de Livro, 589 pp.
- Lydekker, R. 1884. Indian Tertiary and Post-Tertiary Vertebrata. Siwalik and Narbada Carnivora *Paleontologia Indica, Ser. 10*, 2:178-355.
- . 1885. Catalogue of the Fossil Mammalia in the British Museum (Natural History). Part I. Containing the orders Primates, Chiroptera, Insectivora, Carnivora, and Rodentia. London, xxx + 268 pp.
- MacFadden, B., O. Siles, P. Zeitler, M.M. Johnson, and K.E. Campbell, Jr. 1983. Magnetic polarity stratigraphy of the middle Pleistocene (Ensenadan) Tarija Formation of southern Bolivia. *Quaternary Research* 19(2):172-187.
- Marshall, L.G., R.F. Butler, R.E. Drake, and G.H. Curtis. 1982. Geochronology of type Uquian (late Cenozoic) Land Mammal Age, Argentina. *Science* 216:986-988.
- Matthew, W.D. 1918. Contributions of the Snake Creek fauna; with notes upon the Pleistocene of western Nebraska; American Museum Expedition of 1916. *Bulletin of the American Museum of Natural History* 38:183-229.
- Méndez-Alzola, R. 1934. Craneografía y craneometría de *Smilodon bonaerensis* (Muñiz). Trabajo premiado por la institucion Mitre con el permio Carlos Pellegrini para Biología y Ciencias Naturales, Bueno Aires.
- . 1941. El *Smilodon bonaerensis* (Muñiz) estudio osteológico y osteométrico del gran tigre fósil de la pampa comparado con otros félidos actuales y fósiles. *Anales*

- del Museo nacional de historia naturales, "Bernardino Rivadavia," Ciencias Zoológica XL:135-252.
- Merriam, J.C., and C. Stock. 1932. The Felidae of Rancho La Brea. Carnegie Institution of Washington Publications 422:1-232.
- Mones, A., and J.C. Francis. 1973. Lista de los vertebrados fosiles del Uruguay, II. Mammalia. Com. Paleont. Mus. Hist. Natur. de Montevideo 1(4):39-97.
- Muñiz, F.J. 1845. Descripcion del *Munifelis bonaerensis*. Gaceta Mercantil, Buenos Aires, 9(6603).
- Pascual, R., E.J. Ortega Hinojosa, D. Gondar, and E. Tonni. 1966. Paleontografía Bonaerense. Fasciculo IV: Vertebrata. Comision de Investigacion Científica—La Plata, Argentina, 1-202.
- Patterson, B., and R. Pascual. 1972. The fossil mammal fauna of South America; pp. 279-309 in Keast, A., Eck, F.C. and Glass, B. (eds.) Evolution, Mammals, and Southern Continents. State University of New York Press, Albany, New York.
- Paula Couto, C. de. 1940. Carnívoros e Desdentados fósseis de Brasil. Anais III, Congreso, Sul-Riograndense Historia e Geografia 3:1751-1799.
- . 1945. Mamíferos fósseis do Brasil (Carnívoros—Felidae). Revista Instituto historico geográfico do Rio Grande do Sul 25(4):245-261.
- . 1950. Revisão e comentários em Memórias sobre a Paleontologia Brasileira, de P.V. Lund. Instituto Nacional do livro, Rio de Janeiro, 591 pp.
- . 1953. Paleontologia Brasileira (Mamíferos). Ministério da Educação e saúde Instituto Nacional do livro, Rio de Janeiro, 516 pp.
- . 1955. O "Tigre-Dentes-de-Sabre" do Brasil. Boletín conselho Nacional de Pesquisas, Instituto Brasileiro de Bibliografia e Documentacao, Rio de Janeiro, 5-30.
- Pictet, F.J. 1853. Traité de Paléontologie, ou histoire naturelle des animaux fossiles considérés dans leur rapports zoologiques et géologiques, 2 ed., 4°, 1:xiv + 584 pp.
- Robertson, J.S. 1976. Latest Pliocene mammals from Haile XVA, Alachua County, Florida. Bulletin of the Florida State Museum, Biological Sciences 20(3):111-116.
- Rosenzweig, M.L. 1966. Community structure in sympatric carnivores. Journal of Mammalogy 47:602-612.
- Rusconi, C. 1929. Enumeración sistemática de las especies de mamíferos procedentes del piso ensenadense hallados por el autor. Buenos Aires: privately printed, M.L. Rañó, 1-15 pp.
- . 1931. Noticias acerca de un esqueleto juvenil perteneciente a los grandes Carnívoros extinguidos: *Smilodon bonaerensis*. Anales de la Sociedad científica argentina, Buenos Aires CXI:1-10.
- . 1936. Distribución de los vertebrados fósiles, del Piso Ensenadense. Boletín de la Academie nacional de Ciencias, Córdoba 33:183-215.
- Simpson, G. G. 1941. Large Pleistocene felines of North America. American Museum of Natural History, Novitates, no. 1136:1-27.
- Slaughter, B.H. 1960. A new species of *Smilodon* from a late Pleistocene alluvial terrace deposit of the Trinity River. Journal of Paleontology 34:486-492.
- . 1963. Some observations concerning the genus *Smilodon*, with special reference to *Smilodon fatalis*. Texas Journal of Science 15:68-81.
- Spillman, F. 1931. Die Säugethiere Ecuadors im Wandel der Zeit. Part I. Universidad Central, Quito, Ecuador, 112 pp.
- . 1938. Die fossilen Pferde Ekuadors der Gattung *Neohippus*. Palaeobiologica 6:372-393.
- . 1948. Beiträge zur Kenntnis eines neuen gravid-graden Riesensteppentieres (*Eremotherium carolinense* gen. et sp. nov.), seines Lebensraumes und seiner Lebensweise. Palaeobiologica 8:231-279.
- Webb, S.D. 1974a. Chronology of Florida Pleistocene mammals; pp. 5-32 in Webb, S.D. (ed.), Pleistocene Mammals of Florida. University of Florida Press, Gainesville, 270 pp.
- . 1974b. The status of *Smilodon* in the Florida Pleistocene; pp. 149-157 in Webb, S.D. (ed.), Pleistocene Mammals of Florida. University of Florida Press, Gainesville, 270 pp.
- Winge, H. 1895. Jordfundne og nulevende Rovdyr (Carnivora) fra Lagoa Santa Minas Geraes, Brasilien. E Museo Lundii 2(4):1-103.

Accepted 15 July 1985.

APPENDIX 1. SOUTH AMERICAN MATERIAL STUDIED

ARGENTINA

MACN Specimens: 46, nearly complete skeleton (type of *S. bonaerensis*); 997, incomplete skull; 1107 humerus; 2354, right ramus with I₁₋₃, C, left tibia; 2838, humerus; 5010, right ramus; 5109, right femur; 5273, skull, right ramus, proximal femur, tibia, ulna; 5822, fragmentary skull (juvenile); 6205, left ramus with C root and P₄-M₁; 6210, right ramus with P₃-M₁; 6234, tibia; 8661, posterior portion of skull; 8682, posterior portion of skull; 8707, right femur; 9446, distal right humerus; 9650, right humerus; 10037, proximal femur; 10485, tibia; 10502, proximal humerus; 10523, radius; 10861, ulna; 11554, right ramus with I₃, C alveolus, P₄-M₁; 12011, rostral fragment; 12393, fragmentary lower I; 12445, C₁; 12474, C fragment; 12532, ramus with M₁₋₂; 12846, skull fragment; 13606, C₁; 13922, occipital fragment; 14165, left maxillary fragment with P₃₋₄; 13206, M₁; 16693, occipital portion of skull; 16692, ulna; 16689, right and left humeri; 16695, proximal and distal portions of left femur; 16697, proximal right radius; 16691, proximal right tibia; 16690, left astragalus; 16694, right metatarsal III; [12846-16694 are probably all from the same individual, the type of *S. (P.) ensenadensis minor*]; 17448, fragmentary C₁, incomplete skull; 18026, right maxillary fragment with P₄; 18051, symphyseal portion of mandible; 18057, skull and mandibles.

MLP Specimens: 10-1, skull and mandibles; 10-2, incomplete skull and mandibles; 10-10, right ramus; 10-13, left humerus; 10-14, left humerus; 10-20, left ulna; 10-22, right radius; 10-23, right radius; 10-33, left tibia; 10-35, left tibia; 10-37, incomplete right scapula; 10-44, pelvis, sacrum, and lumbar vertebrae; 10-47, axis; 10-48, thoracic and lumbar vertebrae, sacrum, pelvis, right femur.

MMP Specimens: 5M, left femur; 21-S, posterior portion of skull;

34-S, left hindlimb (distal tibia and fibula, astragalus, calcaneum, mesocuneiform, ectocuneiform, cuboid, navicular, metatarsal II-V, proximal phalanges and digits I-V, medial phalanges and digits II-V; ungual phalanges I-IV, sesamoids); 227-S, proximal femur; 465-S, left femur; 495-S (a-f), left and right tibiae, distal epiphysis of femur, astragalus, cervical vertebrae V-VI; 652-S, humerus; 765-M (a-g), phalanges; 768-M, M₁, left P₄; 796-M (a-w), portion of skull, vertebrae (atlas, lumbar, sacrum), pelvis, hindlimb (distal femur, fibula, tibia, left and right astragalus, right and left calcaneum, ectocuneiform, cuboid, navicular, right and left metatarsals II, III, IV, V); 1311-M, incomplete skull with right maxillary, parietal and occipital regions partly restored.

AMNH Specimens: 11101, skull and mandible with nearly complete skeleton; 11103, vertebrae and skeletal fragments; 11104, pelvis; 11105, left femur; 11106, right calcaneum.

FMNH Specimens: P 14294, complete mandible and partial skeleton including: atlas, cervical and thoracic vertebrae, ribs, sternum, humeri, left scapula, ulna, radius, scapholunar, unciform, magnum, metacarpal I, proximal, medial and ungual phalanges, pelvis, femora, tibiae, astragali, left metatarsal II, right metatarsals III, IV and V, and patella; P 14271, skull and mandible (partially restored) and partial skeleton including: atlas, cervical, thoracic, and lumbar vertebrae, sacrum, ribs, left humerus, left and right metacarpal II, right metacarpals II and V, left scapholunar, proximal phalanges, pelvis, right fibula, patella, left astragalus and calcaneum; P 14279, left maxillary fragment with P³⁻⁴.

BOLIVIA

MACN Specimens: 1455, left premaxillary and maxillary fragment with I²⁻³, C; 1457, anterior portion of right ramus with C, P₃ alveolus, P₄ (type of *S. (P.) ensenadensis ferox*); 1459, distal left humerus; 1460, right ramus with I₃-M₁, right and left humerus, left tibia, manus (type of *S. crucians*).

BRAZIL

UZH L Specimens: right I², I³, fragmentary right C¹, left metacarpal II and IV, right metacarpal V (type of *S. neogaucus*); left distal meta-

carpal II, phalanges (hindfoot), C¹, right ramus with incisor alveoli, C root, P₄-M₁ (text and figures in Paula Couto, 1955); Winge (1895: 13) lists additional cranial and postcranial material housed in the UZH collections.

BM(NH) Specimens: 18972, left P³⁻⁴ associated with skull figured by Blainville (1855), left femur (diaphysis), right humerus, right ulna, right distal tibia, right astragalus, phalanx, cervical vertebrae, and right calcaneum, all probably from the same individual.

MNH, right side of skull with I¹⁻³, P⁴-M¹, left C, and fragmentary ramus with complete dentition (text and figures in Blainville, 1855).

ECUADOR

EPN Specimens: V.1507, nearly complete skull; V.1903, cervical vertebrae; V.2990, anterior portion of right scapula; V.1902, proximal right radius; V.1899, left magnum; V.1891, right patella; V.1894, right tibia; V.1895, right tibia; V.1896, proximal right tibia; V.1212, right cuboid; V.1893, left metatarsal III; V.1182, right C¹; V.1185, fragment of left maxillary with P³⁻⁴; V.1186, maxillary fragment with right I¹⁻², left I¹⁻³; V.1187, fragment of right maxillary with P⁴; V.1193, right I³; V.1197, fragmentary right I³; V.1195, left I²; V.1183, mandible with left I₂₋₃, P₄-M₁ and right I₂₋₃, C, P₄-M₁; V.1184, right ramus with P₃ alveolus; V.1191, left dP₄ in fragmentary mandible; V.718, fragment of scapula; V.1188, right humerus; V.1189, left scapholunar; V.1190, left metacarpal IV and V, right metacarpal V; V.1206, left metacarpal III; V.1203-04, phalanx I, digit I (forefoot); V.1292, patella; V.1180, left "perone"; V.1198-1202, phalanges (text and figures in Hoffstetter, 1952).

PERU

The extensive Talaran collection of *S. populator* is currently being described by C.S. Churcher (written comm., 1981).

Appendix 2A–C. Measurements and statistics for *Smilodon populator* from North and South America. Abbreviations: a, approximate measurement; AP, greatest anteroposterior dimension; CV, coefficient of variation; N, sample size; OR, observed range of variation; SE, standard error; T, greatest transverse dimension; $\bar{x}$, mean; 1, measurements following Méndez-Alzola, 1941; Hoffstetter, 1952; Churcher, 1967 and this report; 2, measurements following Merriam and Stock, 1932; 3, measurements following Slaughter, 1963 and this report.

	South America ¹								North America ²			
	Ensenadan				Lujanian				Rancholabrean			
	N	$\bar{x} \pm SE$	OR	CV	N	$\bar{x} \pm SE$	OR	CV	N	$\bar{x} \pm SE$	OR	CV
1. Length, premaxillary–condyle	—	—	—	—	3	358.6 $\pm$ 3.18	355.0–365.0	1.54	25	308.6 $\pm$ 0.958	271.4–344.1	7.77
2. Length, premaxillary–inion	—	—	—	—	4	352.3 $\pm$ 10.46	335.0–353.0	5.93	25	336.0 $\pm$ 1.000	292.7–377.9	7.45
3. Length, C ¹ –P ⁴	1	110	—	—	3	121.2 $\pm$ 0.186	121.1–121.6	0.264	24	112.1 $\pm$ 0.330	97.0–126.3	7.08
4. Greatest width, zygomatic arches	—	—	—	—	6	211.8 $\pm$ 5.49	191.0–225.0	0.634	24	208.8 $\pm$ 0.626	182.9–240.1	7.20
5. Palatal width at P ⁴	—	—	—	—	4	128.6 $\pm$ 5.06	117.0–140.0	7.86	24	127.5 $\pm$ 0.298	114.7–135.4	5.62
6. A–P diameter, auditory bulla	—	—	—	—	4	60.3 $\pm$ 2.89	53.7–67.8	9.59	24	54.2 $\pm$ 0.224	46.7–63.9	9.93
7. Greatest width, mastoid processes	3	136.9 $\pm$ 3.89	132.0–144.6	4.92	9	138.9 $\pm$ 3.71	114.4–147.6	8.01	24	134.6 $\pm$ 0.431	122.0–154.3	7.71
8. Greatest width, condyles	3	70.2 $\pm$ 3.02	66.1–76.0	7.33	10	71.7 $\pm$ 1.33	66.1–78.1	5.86	25	65.0 $\pm$ 0.154	57.6–72.3	5.94
9. Length, symphysis–condyle	2	194.5	183.0–206.0	—	9	224.3 $\pm$ 5.00	198.0–242.8	6.63	25	209.5 $\pm$ 0.632	178.3–230.0	7.55
10. Length, diastema (C ₁ –P ₁)	3	54.7 $\pm$ 3.78	50.1–62.0	11.65	3	68.1 $\pm$ 39.32	64.7–70.0	4.37	25	61.7 $\pm$ 0.314	46.3–71.8	12.72
11. Depth, ramus below M ₁	3	36.8 $\pm$ 2.31	32.7–40.7	10.88	8	43.0 $\pm$ 15.21	40.0–49.0	7.81	25	40.3 $\pm$ 0.110	36.0–45.6	6.84
12. Mandibular toothrow length	2	50.5	48.0–53.0	—	3	52.7 $\pm$ 2.05	48.0–57.0	6.59	25	54.1 $\pm$ 0.123	48.3–60.9	5.72
13. Height, angle–coronoid	1	48.5	—	—	6	71.0 $\pm$ 3.60	61.1–84.2	12.43	25	68.9 $\pm$ 0.207	60.3–76.3	7.53

		South America ¹								North America							
		Ensenadan				Lujanian				Irvingtonian ³				Rancholabrean ²			
		N	$\bar{x} \pm SE$	OR	CV	N	$\bar{x} \pm SE$	OR	CV	N	$\bar{x} \pm SE$	OR	CV	N	$\bar{x} \pm SE$	OR	CV
C	AP	2	42.5	—	—	13	44.6 $\pm$ 1.240	37.6–51.3	10.6					24	42.1 $\pm$ 0.537	36.0–46.1	6.25
	T	2	19.1	—	—	13	21.5 $\pm$ 0.103	20.3–24.0	6.27					24	20.6 $\pm$ 0.374	18.0–22.9	8.89
P ₃	AP	—	—	—	—	9	17.2 $\pm$ 0.616	13.7–20.5	10.74					17	17.1 $\pm$ 0.329	15.0–19.7	7.94
	T	—	—	—	—	9	9.4 $\pm$ 0.321	8.4–11.5	10.24					17	9.3 $\pm$ 0.150	8.4–10.6	6.66
P ₄	AP	—	—	—	—	9	40.5 $\pm$ 1.43	38.4–44.4	10.61	1	37.2	—		22	40.1 $\pm$ 0.538	33.4–46.0	6.29
	T	—	—	—	—	9	15.4 $\pm$ 0.258	14.2–16.4	5.03	1	15.6	—		22	16.5 $\pm$ 0.329	14.2–19.9	9.36
M ₁	AP	—	—	—	—	4	5.7 $\pm$ 0.286	5.0–6.2	10.05								
	T	—	—	—	—	4	13.4 $\pm$ 0.314	12.7–13.9	4.69								
C	AP	3	14.2 $\pm$ 0.38	13.5–14.8	4.58	9	16.6 $\pm$ 1.05	15.6–17.8	24.13	3	14.2 $\pm$ 0.087	14.1–14.4	1.07	22	14.7 $\pm$ 0.231	13.0–16.6	7.40
	T	2	10.1	10.0–10.1	—	9	11.2 $\pm$ 0.179	10.0–12.3	4.80	3	9.1 $\pm$ 0.284	8.5–9.6	6.24	22	10.6 $\pm$ 0.413	9.7–12.2	19.22
P ₃	AP	2	12.0	11.4–12.5	—	1	6.0	—	—	4	8.7 $\pm$ 1.02	5.7–10.1	23.40	2	6.2 $\pm$ —	5.7–7.0	—
	T	2	7.4	7.3–7.5	—	1	6.0	—	—	4	6.3 $\pm$ 0.450	5.0–7.0	14.52	2	8.1 $\pm$ —	6.5–9.6	—
P ₄	AP	4	25.5 $\pm$ 0.50	24.2–26.5	3.94	10	27.7 $\pm$ 0.426	26.3–29.7	4.87	3	26.1 $\pm$ 1.47	24.0–28.9	9.72	25	24.6 $\pm$ 0.273	22.5–26.8	5.55
	T	4	10.9 $\pm$ 0.256	10.2–11.4	4.70	9	12.3 $\pm$ 0.206	11.5–13.5	5.08	3	11.1 $\pm$ 0.550	10.1–12.0	8.59	23	11.9 $\pm$ 0.173	10.9–12.8	6.97
M ₁	AP	3	26.3 $\pm$ 1.63	24.5–29.5	10.73	10	28.3 $\pm$ 0.445	25.7–30.0	4.98	4	28.1 $\pm$ 0.564	27.0–29.5	4.01	25	28.7 $\pm$ 0.338	25.9–32.1	5.89
	T	3	13.9 $\pm$ 0.874	12.2–15.0	10.89	10	13.3 $\pm$ 0.137	13.0–14.2	3.26	4	13.1 $\pm$ 0.147	12.2–15.0	9.88	25	14.3 $\pm$ 0.236	12.8–16.1	8.28

		South America ¹								North America ²			
		Ensenadan				Lujanian				Rancholabrean			
		N	$\bar{x} \pm SE$	OR	CV	N	$\bar{x} \pm SE$	OR	CV	N	$\bar{x} \pm SE$	OR	CV
Humerus		2	334.0	—	—	6	365.4 $\pm$ 10.50	340.5–395.0	7.04	10	344.9 $\pm$ 7.80	309.0–385.0	7.13
Radius		1	225.0	—	—	5	275.7 $\pm$ 8.06	249.7–294.8	6.54	10	265.7 $\pm$ 6.84	235.0–295.0	8.14
Metacarpal III		1	95.0	—	—	3	95.4 $\pm$ 1.10	94.3–97.6	2.00	737	—	83.0–107.8	—
Femur		4	352.8 $\pm$ 2.81	347.0–360.0	1.59	4	384.0 $\pm$ 9.17	365.0–408.0	4.78	10	367.7 $\pm$ 9.80	317.0–408.0	8.43
Tibia		7	251.4 $\pm$ 7.86	220.0–282.6	8.27	5	280.4 $\pm$ 4.21	272.5–294.2	3.36	10	273.6 $\pm$ 8.10	239.0–305.0	9.31
Metatarsal III		1	98.5	—	—	4	98.0 $\pm$ 0.595	94.7–99.1	1.21	766	—	85.5–111.5	—